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Spatial patterns and species performances in experimental plant communities

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Abstract Amongst the various hypotheses that challenged to explain the coexistence of species with similar life histories, theoretical, and empirical studies suggest that spatial processes may slow down competitive exclusion and hence promote coexistence even in the absence of evident trade-offs and frequent disturbances. We investigated the effects of spatial pattern and density on the relative importance of intra- and interspecific competition in a field experiment. We hypothesized that weak competitors increased biomass and seed production within neighborhoods of conspecifics, while stronger competitors would show increased biomass and seed production within neighborhoods of heterospecifics. Seeds of four annual plant species (*Capsella bursa-pastoris, Stachys annua, Stellaria media, Poa annua*) were sown in two spatial patterns (aggregated vs. random) and at two densities (low vs. high) in three different species combinations (monocultures, three and four species mixtures). There was a hierarchy in biomass production among the four species and *C. bursa-pastoris* and *S. media* were among the weak competitors. *Capsella* and *Stellaria* showed increased biomass production and had more individuals in the aggregated compared to the random pattern, especially when both superior competitors (*S. annua, P. annua*) were present. For *P. annua* we observed considerable differences among species combinations and unexpected pattern effects. Our findings support the hypothesis that weak competitors increase their fitness when grown in the neighborhood of conspecifics, and suggested that for the weakest competitors the species identity is not important and all other species are best avoided through intraspecific aggregation. In addition, our data suggest that the importance of spatial pattern for the other competitors might not only depend on the position within the hierarchy but also on the identity of neighbor species, species characteristics, below ground interactions, and other nonspatial factors.

Keywords Annual species · Coexistence · Intra- and interspecific competition · Population dynamics

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Introduction

Competition, both within and among species, is one of the major forces determining the distribution and abundance of plant species and the biodiversity of plant communities (Tilman 2000). Although most plants compete for the same resources (light, water, and nutrients), we observe large numbers of coexisting species in many plant communities (Silvertown and Charlesworth 2001). One of the central issues in ecology remains to explain how large numbers of species are able to coexist in natural communities. Many hypotheses have attempted to explain the coexistence of species with similar life histories (see e.g., Chesson 2000; Wright 2002; Shea et al. 2004; Barot 2004). Intuitively, spatial heterogeneity of resources used by plants is probably one of the most powerful promoters of niche separation and coexistence between plants. However, niche separation alone cannot explain the more species-rich communities. Grubb (1977) emphasized the importance of the entire life cycle of an individual and its ability to become established as part of the environment, which has recently become vacant (regeneration niches). Another classical mechanism explaining coexistence is based on the existence of a trade-off between colonization and competitive ability: good competitors must be poor colonizers and vice versa (Tilman 1994; Levine and Rees 2002). In that case coexistence occurs because

species with sufficiently high dispersal rates persist in sites not occupied by superior competitors. Recent studies provided empirical evidence for the importance of such trade-offs in communities of sand-dune annuals (Rees 1995; Turnbull et al. 1999, 2004). Moreover, such trade-offs are particularly important if disturbances remove strong competitors and create new gaps for colonization (Connell 1978; Huston 1979). However, explaining species coexistence in the absence of conspicuous life-history trade-offs and in relatively homogeneous environments remains challenging and controversial (see e.g., Amarasekare 2003; Barot 2004).

As a consequence of the limited seed dispersal and/or clonal growth, most plant species create aggregations of conspecifics, thereby increasing the importance of intraspecific competition relative to interspecific competition (spatial segregation hypothesis, Pacala 1997). This is particularly relevant to plant communities because most of the ecological and genetic interactions between individual plants are with their immediate neighbors. Therefore, survivorship and fecundity are affected more by local population density than by the average density of the population (Pacala and Silander 1985; Pacala 1997; Stoll and Weiner 2000; Murrell et al. 2001). There is a large body of theories that underlines the importance of spatial pattern for ecological phenomena, for example coexistence and maintenance of biodiversity (Kareiva 1990; Bergelson 1990; Rees 1995; Rees et al. 1996; Murrell et al. 2001; Coomes et al. 2002; Bolker et al. 2003; Levine and Murrell 2003). Indeed, one proposed mechanism promoting coexistence is that intraspecific aggregation caused by limited seed dispersal and local interactions might slow down competitive exclusion. Although spatial theory has made great strides in advancing the understanding of coexistence in patchy environments, progress on the empirical front has been comparatively slow and an experimental validation of spatial ecology is still largely missing (see e.g., Rejmánek 2002; Amarasekare 2003; Bolker et al. 2003). Nevertheless, an early experimental study (Schmidt 1981) with two clonal perennials showed that after 3 years, interspecific competition was reduced and coexistence of competitors facilitated, in intraspecifically aggregated populations. Bergelson (1990) in an experiment with *Capsella bursa-pastoris* and *Senecio vulgaris* showed that the performance of *Capsella* and *Senecio* was much higher when grown in a patchy matrix of *Poa annua* than in a matrix of randomly distributed *Poa*. Recently, Stoll and Prati (2001) tested the prediction, made from spatial competition models, that aggregation may promote coexistence by slowing down competitive exclusion and thus maintain biodiversity. Using an experimental plant community composed of four annual species, they showed that the spatial pattern of individuals altered the competitive interactions in plant communities and facilitated coexistence at least in the short term. In particular, they found that weaker competitors increased the above ground biomass when intraspecifically aggregated, especially at high density where competition was greater than at low density. On the other hand, competitively superior species produced lower biomass in the aggregated pattern than in the random pattern at high density. Other studies showed similar pattern effects on plant population dynamics (Harper et al. 1961; Brophy and Mundt 1991; Stauber et al. 1991; Norris et al. 2001). Nevertheless, there are still controversial views over what permits competitors to coexist in the absence of conspicuous life-history trade-offs and frequent disturbances (e.g., Neuhauser and Pacala 1999; Wright 2002; Levin and Murrell 2003; Amarasekare 2003; Barot 2004). Moreover, as empirical and experimental evidence of effects of intraspecific aggregation on species interactions is still poor, the question whether or not intraspecific aggregation of species prevents or promotes coexistence remains open (Chesson 1991; Chesson and Neuhauser 2002; Murrell et al. 2002; Bolker et al. 2003). Indeed, the simplistic view of aggregation as a mechanism of coexistence of plant species proposed by some studies (e.g., Pacala 1997; Pacala and Levin 1997; Murrell et al. 2001, 2002) has been criticized and the importance of trade-offs between life-history parameters (Bolker and Pacala 1999) in the explanation of plant species coexistence has been stressed (Chesson and Neuhauser 2002). In response to Chesson and Neuhauser (2002), Murrell et al. (2002) gave an example in which the spatial extension of a nonspatial model allowed coexistence of two species even without trade-offs. Furthermore, Murrell and Law (2003) using an explicitly spatial versions of the Lokta-Volterra model showed that weaker competitors were able to coexist with their stronger rivals when interspecific interactions occurred over shorter distances than intraspecific interactions (heteromyiopia). Thus, as the authors suggested, it is most likely that there are some conditions under which spatial structure promotes coexistence and others under which it does not.

The aim of the present experiment was to evaluate the effects of spatial pattern and density on the relative importance of intra- and interspecific competition on plant dynamics. This experiment expands the pilot experiment of Stoll and Prati (2001) and differs in three ways: (1) it relies on more natural conditions (not steam sterilized soil and less weeding), (2) plants grew on a heavy soil with high clay content, and (3) substitutes a common annual species (*Cardamine hirsuta*) with a rare annual species (*Stachys annua*). In both experiments the four plant species were annuals with different morphologies. Based on the pilot experiment we hypothesized that spatial pattern may affect the growth and the fitness of plant species in such a way that weaker competitors may benefit (i.e., would show increased biomass and seed production) in an aggregated compared to a random pattern, while stronger competitors would show increased fitness in random compared to aggregated patterns. Furthermore, as overall density of plants generally affects the intensity of competition, we expected the effect of intraspecific aggregation to be more evident at higher densities.

Materials and methods

We investigated the effects of spatial pattern and density on plant performance and community dynamics in a field experiment (at the Research Institute of Organic Agriculture (FiBL), Frick, Switzerland) using four annual plant species with different morphologies. *Capsella bursa-pastoris* L. (Brassicaceae) is a rosette-forming plant with a multiflowered erect stem up to 40-cm-high. *Poa annua* L. (Poaceae) has adventitious roots at the first nodes and tillers up to 30-cm-high. *Stellaria media* L. (Caryophyllaceae) is prostrate to ascending, with high adventitious rooting and a height of up to 40 cm. *Stellaria* and *Poa* are widely distributed, cosmopolitan annuals of disturbed habitats. *Stachys annua* L. (Lamiaceae) has a multiflowered erect stem up to 40-cm-high. Compared to the other three species, *S. annua* is quite rare in most parts of Europe. Moreover, members of the Brassicaceae (e.g., *Capsella*) and Caryophyllaceae (e.g., *Stellaria*) are usually considered nonmycorrhizal, while members of the Poaceae (e.g., *Poa*) and Lamiaceae (e.g., *Stachys*) are generally mycorrhizal (Harley and Harley 1987; Smith and Read 1997).

The experiment was designed as a split-plot and contained 2 blocks (0.6 m×8 m, separated by 0.5 m), established between May 20 and 24 and harvested in the fall of 2002. Each block was subdivided into an upper- and lower subblock (Fig. 1). During the first 2 months the two blocks were covered with a plastic tunnel (200 holes/m^2, GVZ-Bolltec AG, Zürich, Switzerland) to protect the seedlings from adverse weather and full sunlight. Each block contained eight main plots (0.6 m×0.6 m, separated by 0.3 m). Spatial pattern and density were used as plot-level treatments and each treatment was replicated twice per block and randomly assigned to plots (Fig. 1). The plots were sown between May 30 and June 4 and watered each evening until May 6; thereafter, an automatic irrigation system (Gardena AG, Bachenbülach, Switzerland) was installed. The system was programmed to give rain cycles lasting 1 min (i.e., 1 l water) starting at 5:15, 6:15, 7:15 a.m., and 7:15, 8:15, and 9:15 p.m. The duration of the 8:15 p.m. rain cycle was changed from 1 min to 2 min on June 25.

The combinations of mixtures of species (see below) and monocultures were used as within-plot treatments. The plots were subdivided into nine subplots (0.2 m×0.2 m), each of which contained either one of the four species in monoculture, one of the four possible three-species mixtures, or the four-species mixture (Fig. 1). In the random pattern, seeds of each species were sown over the subplots so that in the mixtures, the individuals experienced inter- and intraspecific encounters at the same frequency. In the aggregated pattern, the subplots were further subdivided into 16 cells (5 cm×5 cm), and each cell contained only one of the species in such a way that individuals experienced more intra- than interspecific encounters (Fig. 1). The species were randomly allocated to the cells. In the four-species mixture, each species occupied four cells, whereas in the three-species mixtures, each species occupied five cells and one-third of the sixteenth cell. At low density, we sowed 10 seeds per cell (4,000 seeds/m^2) whereas at high density we sowed 100 seeds per cell (40,000 seeds/m^2). After sowing, in order to increase germination, the seeds were covered by a layer (2 cm) of commercial garden soil, instead of the heavy soil (high clay content), and pressed down slightly to prevent the seeds from being washed away. The seeds were obtained from a commercial supplier (Herbiseed, Wokingham, Berkshire, UK) and counted using a mechanical seed counter (Elmor). Hundred seeds for each species were weighted to determine the mean seed weight.

A snail fence enclosed the entire experimental field and slug pellets were regularly used to curtail herbivory.

The above-ground biomass was harvested between August 20 and September 29, and the total number of individuals per species was counted. For *Poa* we counted ramets rather than genets. When the total number of individuals per species exceeded ten, we randomly selected ten individuals, measured their height, and separated vegetative from reproductive parts. We only separated vegetative from reproductive biomass for the remaining plants. Almost all individuals of *Stellaria*, *Capsella*, and *Stachys* produced flowers, while only few *Poa* flowered. The harvested biomass was dried at 60°C for 48 h in Frick and then stored. Before it was weighed the biomass was dried again for 17 h at 60°C.

Since the fixed automatic irrigation system might have affected the above-ground biomass production we tested (1) the correlation between the amount of water supplied by the fixed automatic irrigation system and total biomass of all fours species produced at the subplot level and (2) the effects of both factors by using an analysis of covariance. As no correlation was found and since the total biomass of all four species produced at the subplot level showed a significant covariate effect, we decided to use the total biomass as indirect measure to quantify the effects of the fixed irrigation system and other unknown factors. Since the main treatments (pattern and density) varied at the plot rather than at the subplot level, the covariate should not be confounded with the main treatments.

The data were analyzed with multifactorial analysis of covariance (ANCOVA). The main effects (pattern, density) and their interaction were tested against the plot-level residual mean square. When the effect of the species mixtures combinations was significant, we used linear contrasts to separate them into (1) the difference between monoculture and mixtures and (2) difference between the three- and four-species mixtures.

In the cases where the design became unbalanced because of missing values (i.e., subplot where plants did not grow), we used regression analysis or performed the analysis either without the corresponding subplots or restricted the analysis to the high density. In the particular case for *Capsella* and *Stellaria* when the analysis was restricted to the species combinations with *Stachys*

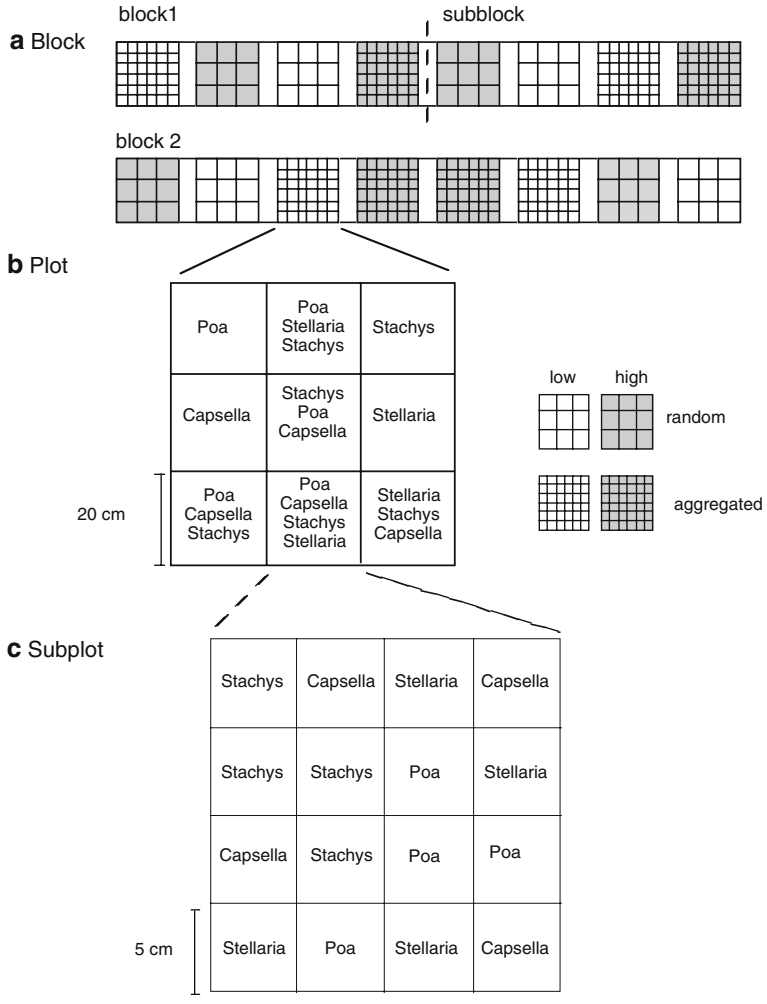

Fig. 1 The experimental design. **a** Two blocks each containing four plots at either high or low density and random or aggregated pattern, twice replicated per treatment and species mixtures $n = 4$. **b** Plots subdivided into nine subplots, each containing either a monoculture, one of the possible three- or four-species mixture. **c** An example of the intraspecifically aggregated pattern. In the four-species mixture each species occupied a single cell. In the random pattern the corresponding number of seeds of all species was distributed throughout the 20 cm×20 cm subplot

and *Poa*, there were at the low-density two missing values: four species mixture/random pattern and four species mixture/aggregated pattern. As the results of the analysis changed significantly depending on whether we considered those missing values as 'true zero' or left them out, we decided to present both results. Generally we did the analysis without the factor 'subblock' because it was not significant. However, for *Poa* we integrated it in the analysis for the vegetative biomass, number of individuals, and the coefficient of variation (CV) in length because it had a significant effect. Using the ten selected individuals, the CV in length, vegetative, and reproductive biomass was evaluated to assess the mode of competition (i.e., symmetric vs. asymmetric).

The data were calculated as grams per square meter and log-transformed to obtain normal distribution of the residuals and homogeneity of variances. Back-transformed means and standard errors from the analysis are presented throughout.

All analyses were conducted using the program GENSTAT 5 (Payne et al. 1987).

Results

Stachys annua had the heaviest seeds, followed by *S. media*, *Poa annua*, and *Capsella bursa-pastoris* with the lightest seeds. *Stachys* produced the highest biomass, followed by *Poa*, *Capsella*, and *Stellaria* (Table 1).

The spatial pattern affected the growth and the fitness of *Capsella*, and to some extent, *Stellaria*, in such a way that there was an increase in biomass, seed production, and number of individuals in the aggregated compared to the random pattern.

The analysis for *Capsella*, excluding the monoculture, showed higher biomass in the aggregated (vegetative = 167.11 g/m^2; reproductive = 19.86 g/m^2) compared to the random pattern (vegetative = 100.23 g/m^2;

Table 1 Seed mass and total above-ground biomass for the four experimental species

Species	Seed mass (mg/100 seeds)	Total above-ground biomass (g/m^2)
Stachys annua	113.0	637.8
Stellaria media	42.8	172.8
Poa annua	32.3	559.8
Capsella bursa-pastoris	9.8	202.4

reproductive = 9.46 g/m^2) (Table 2). In addition, the total number of individuals was significantly higher in the aggregated (851.14 ind/m^2) compared to the random pattern (527.23 ind/m^2) (Table 2). These spatial pattern effects were only marginally significant for both vegetative and reproductive biomass, yet they were more pronounced in the species mixtures with *Stachys* and *Poa* (Table 2, Fig. 2). In this case, vegetative biomass of *Capsella* increased by 186% and reproductive biomass by 126% within neighborhoods of the same species, which corresponded to an increase of about roughly 10,000 seeds/m^2 (Fig. 2).

Capsella in the species combinations together with *Stachys* and *Poa* at the high-density treatment showed significantly higher CV for length in the aggregated (81%) compared to the random pattern (63.9%) ($F_{1,4} = 13.85$, $P = 0.020$).

For *Stellaria* the positive effects of aggregation occurred only in those mixtures where *Stachys* and *Poa* were present (Table 3). *Stellaria* increased the vegetative biomass by 288% and the reproductive biomass by 280% in the aggregated compared to the random pattern (Fig. 2). *Stellaria* did not show any significant differences in size variation between patterns.

The analysis for *P. annua*, including all combinations, showed significantly higher vegetative biomass in the aggregated compared to the random pattern (Table 4). In addition, we found highly significant differences among the species combinations (Table 4). The linear contrasts indicated that this effect was due to the differences between the four- and three-species mixtures ($F_{1,4} = 6.27$; $P = 0.016$). Moreover, they showed significant differences among three species mixtures with *Stachys* and without *Stachys* ($F_{1,4} = 10.58$; $P = 0.002$) (Fig. 3).

The total number of individuals of *Poa* differed significantly among species combinations (Table 4). The calculated linear contrasts showed that the differences were again due to the differences between the species mixture and the monoculture ($F_{1,4} = 9.09$; $P = 0.004$) and among three-species mixtures with *Stachys* and without *Stachys* ($F_{1,4} = 14.95$; $P = < 0.001$).

Although we restricted our analysis to the high-density treatment due to the missing values present at the low-density treatment, for *S. annua* we found neither treatment effects nor species combinations effects or significant interactions.

Table 2 Results of ANCOVA for *C. bursa-pastoris* testing effects of spatial pattern, density, and species combinations on above-ground biomass production and number of individuals

Source of variation	df	Vegetative biomass		Reproductive biomass		Number of individuals	
		F values	*P* values	*F* values	*P* values	*F* values	*P* values
Excluding monoculture							
Block	1	0.07	0.835	0.11	0.796	0.05	0.861
Pattern (P)	1	3.91	0.076	4.49	0.060	9.30	**0.012**
Density (D)	1	0.59	0.460	0.89	0.367	23.37	**< 0.001**
P×D	1	0.00	0.983	0.26	0.621	0.98	0.977
Covariate	1	10.42	**0.009**	11.30	**0.007**	2.45	0.149
Plot level	10	1.83		1.76		2.27	
Combinations (C)	3	0.96	0.423	0.7	0.561	0.35	0.793
P×C	3	0.47	0.703	0.53	0.664	0.68	0.569
D×C	3	0.63	0.602	0.52	0.672	2.24	0.101
P×D×C	3	0.38	0.769	0.33	0.801	0.19	0.901
Covariate	1	15.60	**< 0.001**	22.00	**< 0.001**	0.05	0.824
Residual	35						
Restricted to the species combinations with *S. annua* and *P. annua*							
Block	1	0.00	0.980	0.01	0.936	0.25	0.705
Pattern (P)	1	4.36	0.063	5.15	**0.047**	2.57	0.140
Density (D)	1	0.04	0.850	1.87	0.202	7.82	**0.019**
P×D	1	0.09	0.771	0.16	0.696	0.07	0.794
Covariate	1	18.31	0.002	20.20	0.001	0.00	0.950
Plot level	10	1.84		1.84		3.37	0.488
Combinations (C)	1	0.47	0.505	0.7	0.419	0.51	0.888
P×C	1	0.44	0.521	0.43	0.524	0.02	0.069
D×C	1	0.42	0.532	1.2	0.297	4.05	0.505
P×D×C	1	0.72	0.415	0.58	0.463	0.48	0.371
Covariate	1	12.68	**0.004**	22.90	**< 0.001**	0.87	
Residual	31						

Covariate: total above-ground biomass of the four experimental species at the subplot level

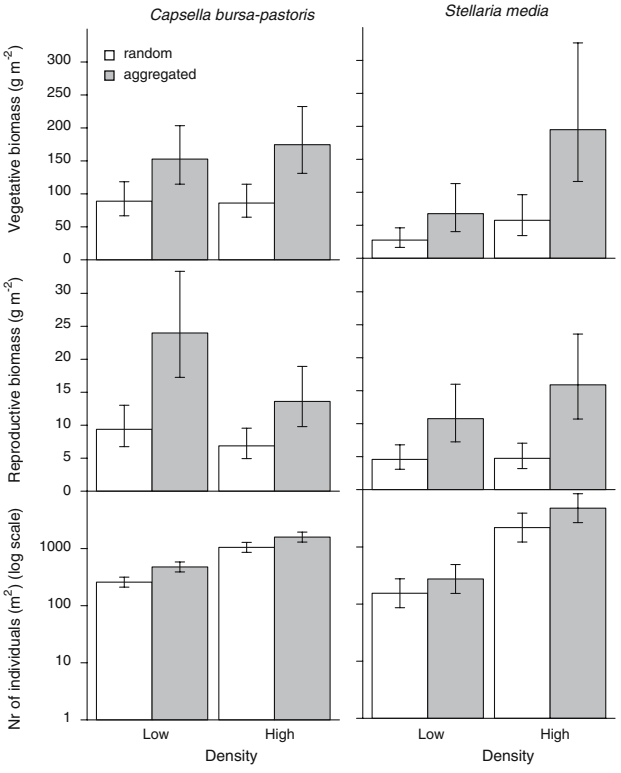

Fig. 2 Above-ground biomass and number of individuals of *Capsella bursa-pastoris* and *Stellaria media* restricted to the species combinations with *Stachys annua* and *Poa annua*. *White bars*: random pattern, *grey bars*: aggregated pattern. The *bars* represented back-transformed means ±1 SE from ANCOVA of log-transformed data

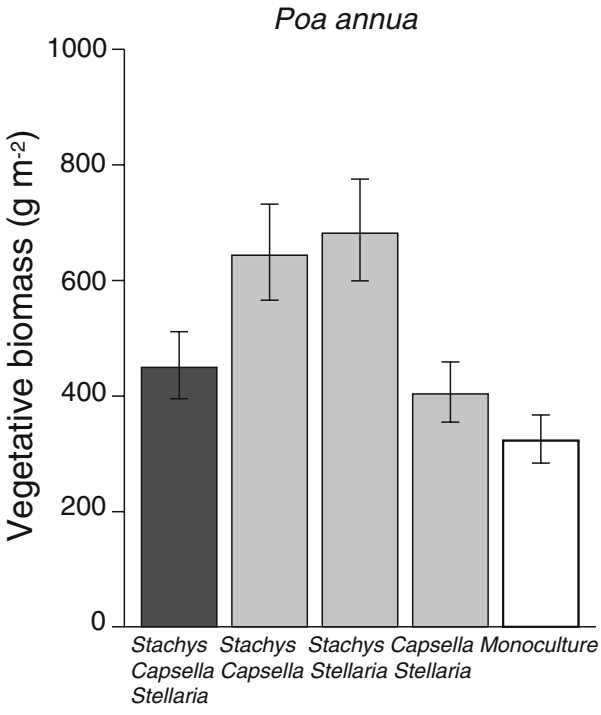

Fig. 3 Total vegetative biomass of *P. annua* on various combinations averaged over the treatments and densities. The *bars* represented back-transformed means ±1 SE from ANCOVA of log-transformed data

Discussion

Our experiment provided evidence that spatial pattern affected growth and reproduction of plants within an experimental community in a short run. Our results showed that compared to a pilot experiment (Stoll and Prati 2001), using a slightly 'different' experimental plant community and soil treatment, not only did the competitive hierarchy change, but so did the spatial pattern effects for the individual species. Our data on *C. bursa-pastoris* and, to some extent *S. media*, were consistent with the pilot experiment and support the hypothesis that weak competitors may increase their fitness (e.g., survival and seed production) within neighborhoods of

Table 3 Results of ANCOVA for *S. media* testing effects of spatial pattern and density on above-ground biomass production and number of individuals limited to the species combinations with *S. annua* and *P. annua*. ANCOVA with missing values ($n = 2$) replaced with a '0'. Covariate: total above-ground biomass of the four experimental species at the subplot level

Source of variation	df	Vegetative biomass		Reproductive biomass		Number of individuals	
		F values	*P* values	*F* values	*P* values	*F* values	*P* values
Block	1 (1)[a]	1.40 (0.06)	0.447 (0.847)	3.91 (0.86)	0.298(0.524)	3.06 (0.02)	0.331 (0.911)
Pattern (P)	1 (1)	4.37 (2.19)	0.063 (0.177)	6.15 (3.42)	**0.033**(0.102)	2.60 (2.30)	0.138 (0.168)
Density (D)	1 (1)	3.29 (1.33)	0.100 (0.282)	0.31 (0.03)	0.589 (0.878)	23.85 (37.94)	**<0.001 (<0.001)**
Combinations (C)	(1)	(0.08)		(0.09)	(0.776)	(0.14)	(0.714)
P×D	1 (1)	0.10 (0.36)	0.755 (0.788)	0.23 (0.48)	0.644 (0.507)	0.03 (0.10)	0.867 (0.758)
P×C	(1)	(3.07)	(0.567)	(3.79)	(0.087)	(0.37)	(0.561)
Covariate	1(1)	8.51 (6.50)	**0.015 (0.034)**	10.29 (6.84)	**0.009 (0.031)**	2.05 (1.19)	0.183 (0.307)
Plot level	10 (8)	0.89 (0.90)		0.75 (0.85)		1.03 (1.22)	
C	1 (1)	3.64 (2.18)	0.083 (0.174)	0.82 (0.68)	0.385 (0.432)	3.11 (1.31)	0.105 (0.281)
P×C	1 (1)	0.21 (0.04)	0.659 (0.851)	0.03 (0.05)	0.867 (0.829)	0.13 (0.56)	0.722 (0.473)
D×C	1 (1)	1.54 (0.15)	0.240 (0.704)	0.01 (0.15)	0.944 (0.705)	3.50 (0.87)	0.088 (0.375)
P×D×C	1 (1)	0.00 (0.39)	0.968 (0.545)	0.14 (1.26)	0.716 (0.290)	0.00 (0.09)	0.985 (0.770)
Covariate	1 (1)	2.01 (5.13)	0.184 (**0.050**)	4.63 (7.92)	0.055 (**0.020**)	0.22 (0.04)	0.647 (0.842)
Residual	11 (9)						

[a]Number in brackets ( ) represented results of ANCOVA excluding the missing values

Table 4 Results of ANCOVA for *P. annua* testing effects of spatial pattern, density, and species combinations on above-ground biomass production and number of individuals. Covariate: total above-ground biomass of the four experimental species at the subplot level

Source of variation	df	Vegetative biomass		Number of individuals	
		F values	*P* values	*F* values	*P* values
Block	1	1.61	0.332	0.63	0.511
Subblock	2	16.38	**0.003**	14.15	**0.004**
Pattern (P)	1	5.97	**0.040**	2.12	0.184
Density (D)	1	3.21	0.111	27.42	**<0.001**
P×D	1	0.00	0.985	0.03	0.869
Covariate	1	4.82	0.059	2.41	0.159
Plot level	8	1.41		1.52	
Combinations (C)	4	6.32	**<0.001**	6.64	**<0.001**
P×C	4	0.22	0.925	0.53	0.712
D×C	4	0.74	0.568	2.37	0.066
P×D×C	4	0.69	0.601	0.77	0.551
Covariate	1	1.74	0.194	0.25	0.621
Residual	47				

conspecifics compared to neighborhoods of heterospecifcs, especially when the superior competitors were present in the community. Moreover, data on *Stellaria* (which was the strongest competitor in the pilot experiment, see below) suggested that for the weakest competitors the species identity is not important and all other species are best avoided through intraspecific aggregation. In addition, our findings for *P. annua* revealed considerable differences among species mixture and unexpected pattern effects. This suggests that the importance of spatial pattern might not only depend on competitive hierarchies, and aggregation might be beneficial, because there may be positive interactions (e.g., complimentarity, mutualisms) associated with some of the other species.

Based on the total above-ground biomass production, our results suggest two 'main groups': one composed of *S. annua* and *P. annua* as strong competitors and one group composed of *C. bursa-pastoris* and *S. media* as weak competitors.

Capsella was among the weaker competitors both in the pilot and the present experiment and showed increased biomass production and number of individuals in the aggregated compared to the random spatial pattern, especially in combination with the competitively superior species. By contrast, *Stellaria* was the strongest competitor in the pilot and a weak competitor in the present experiment. Although this species only partly confirmed our hypothesis, the data suggest a benefit of intraspecific aggregation, once again in combination with the competitively superior species. Note that in the pilot experiment *Stellaria* produced more above-ground biomass in the random compared to the aggregated pattern, while in the present experiment behaved like the other weak competitor *Capsella*. Our results are quite remarkable because they not only show the positive advantage of intraspecific aggregation for weak competitors, but also that these advantages do not seem to depend on species identity.

Our data about the two superior competitors *Stachys* and *Poa* do not agree, however, with the pilot experiment, where superior competitors were suppressed in the neighborhood of conspecifics. In fact, neither *Stachys* nor *Poa* increased their biomass in the random pattern. Furthermore, contrary to our expectations, the superior competitor *Poa* increased the vegetative biomass in the aggregated pattern as opposed to the random pattern. These results were unexpected and quite difficult to explain. For *Stachys* it is possible that the high data variability and the rather high number of missing values present in the low-density treatment may have masked a possible treatment effect. On the other hand, our findings on *Poa* were similar to results found in a study with two perennial grasses where the superior competitive ability of *Agropyron* did not emerge based on the relative performance of this species in monoculture and mixture (Huber-Sannwald et al. 1996).

Besides, *Poa* showed different responses depending on community composition. *Poa* generally increased its fitness (i.e., vegetative biomass and number of individuals) if associated with the other superior competitor *Stachys*. This result could be explained with some complimentarity of species' traits and/or below-ground mutualisms (see below). Findings on *Poa* suggest that the position of a species within a community hierarchy is not sufficient to predict effects of spatial pattern and that the importance of spatial pattern might depend on which species composed the communities.

In contrast to Stoll and Prati (2001), we observed another plant hierarchy in the community, which might be explained by (1) different species composition; (2) different soil treatment, and (3) trade-offs. *Stellaria*, which was the strongest competitor in the pilot experiment, turned out to be the weakest in the present experiment. *Poa* changed its position from the second weakest to the second strongest competitor. Performances of *Capsella* did not vary between the two experiments and it remained as third weakest competitor. The newly introduced species, *Stachys*, was the strongest competitor. Intuitively, the substitution of *C. hirsuta* (a rosette-forming plant of the Brassicaceae) used in the pilot experiment with *Stachys* used in our experiment could have changed the competitive interactions between the experimental plant species leading to a new plant hierarchy. However, the different soil treatments, which were a steam-sterilized nutrient-rich garden soil in the pilot experiment and an unsterilized heavy soil with high clay content in the present experiment, might also explain the different hierarchies. Therefore, the presence or absence of mycorrhizal fungi in the soil could have played an important role in determining the community structure (van der Heijden et al. 1998, 2003). There is growing evidence that the below-ground biota (e.g., mycorrhizal fungi) play an important role in determining the community structure and coexistence of competitors (e.g., Hartnett and

Wilson 1999; Klironomos et al. 2000; Klironomos 2002; Bever 2003). Recently, Hart et al. (2003) reviewed the importance of arbuscular mycorrhizal fungi (AMF) in mediating plant coexistence. For example, West (1996) showed that if a highly competitive plant species is more infected by AMF, then AMF would simply reinforce competitive dominance of that species. Based on those considerations and the mutualism and antagonism in the mycorrhizal symbiosis and the impact on plant community (Francis and Read 1995), we speculate that the two superior competitors in our experiment might have experienced a kind of belowground mutualism between each other. However, some studies (DeMars and Boerner 1994; Ishii et al. 1998), have reported some vesicular–arbuscular mycorrhizal infection also in members of the Brassicaceae and Caryophyllaceae. Although these authors suggested that the mycorrhizas might be nonfunctional, we cannot exclude possible root interactions between our experimental plants species.

Nevertheless, also the competition/colonization trade-off (Tilman 1994; Rees 1995; Turnbull et al. 1999, 2004) could in part explain the different plant hierarchies. As expected the large-seeded *Stachys* was one of the superior competitors, while the small-seeded *Capsella* was one of the inferior competitors. By contrast, the second large-seeded (*Stellaria*) and the second small-seeded (*Poa*) were the second weakest competitor and the second strongest competitor, respectively. This suggests that the performance (i.e., competitive ability) of a plant species and therefore its position in a given hierarchy is not simply correlated with the seed size. Indeed, when appropriate biological details are included in theoretical models, the performance of individuals varies in response to other factors such environmental heterogeneity and competition with surrounding neighbors. Furthermore, there is evidence that high-competitive asymmetries in addition to competition/colonization trade-off are needed to explain coexistence (Adler and Mosquera 2000; Levine and Rees 2002). Recently, in a review about colonization, tolerance, competition, and seed-size variation, Coomes and Grubb (2003), stressed the limits on the potential of competition/colonization trade-off to allow long-term coexistence without other forms of niche differentiation. So far it remains an open question to which extent seed size, in particular the competition/colonization trade-off together with spatial pattern (i.e., intraspecific aggregation), might benefit weak competitors and hence allow long-term coexistence by slowing down competitive exclusion (see e.g., Turnbull et al. 2004).

In contrast to the pilot experiment, we could not find any interactions between density and spatial pattern. Hence, our hypothesis that the spatial pattern effect should be more evident at high density because of the higher intensity of competition must be rejected. However, we suspect that the high variability of our data might have hidden such interactions, and thus complicated the interpretation of the outcomes.

This huge variability could be partially explained by the fixed automatic irrigation system, which systematically irrigated some subplots more than others. In consideration of the fact that we did not find a direct correlation between the amount of water and the total biomass of all four species produced for each subplot, we assume that the fixed irrigation system was not the only reason for the observed variability. For instance, other factors such as the high soil water storage capacity may have favored some species and killed others.

In conclusion, we showed that spatial pattern affected an experimental plant community at least in the short run. Moreover, our findings supported the hypothesis that weaker competitors might increase their fitness (e.g., biomass and seed production) within neighborhoods of consepecifics compared to neighborhoods of heterospecifics. Furthermore, our data suggested that the advantages of intraspecific aggregation for weaker competitors might be independent of species identity and that all other species are best avoided. In addition, our findings on *P. annua* revealed considerable differences among species mixture and unexpected pattern effects. This suggests that the importance of spatial pattern might not only depend on competitive hierarchies, and aggregation might be beneficial because there may be positive interactions (e.g., complimentarity, mutualisms) associated with some of the other species. Although we did show that spatial pattern had an impact on the plant population dynamics, it remains unclear as how important these processes are relative to other nonspatial factors. In addition, more long-term experiments are needed in order to understand whether or not intraspecific aggregation promotes coexistence by retarding competitive exclusion. Accordingly, further studies are needed to better comprehend under which conditions the spatial pattern will affect the dynamics of a given plant community and under which conditions it may be ignored. On the other hand, a better knowledge of spatial pattern and plant population dynamics is needed in order to build predictive models and address more fundamental questions, such as the prediction of the importance, rather whether or not, a mechanism may promote coexistence in plant communities.

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